Signature-whistle production in undisturbed free-ranging bottlenose dolphins (*Tursiops truncatus*)

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Data from behavioural observations and acoustic recordings of free-ranging bottlenose dolphins (*Tursiops truncatus*) were analysed to determine whether signature whistles are produced by wild undisturbed dolphins, and how whistle production varies with activity and group size. The study animals were part of a resident community of bottlenose dolphins near Sarasota, Florida, USA. This community of dolphins provides a unique opportunity for the study of signature-whistle production, since most animals have been recorded during capture–release events since 1975. Three mother–calf pairs and their associates were recorded for a total of 141.25 h between May and August of 1994 and 1995. Whistles of undisturbed dolphins were compared with those recorded from the same individuals during capture–release events. Whistles were conservatively classified into one of four categories: signature, probable signature, upsweep or other. For statistical analyses, signature and probable signature whistles were combined into a 'signature' category; upsweep and other whistles were combined into a 'non-signature' category. Both 'signature' and 'non-signature' whistle frequencies significantly increased as group size increased. There were significant differences in whistle frequencies across activity types: both 'signature' and 'non-signature' whistles were most likely to occur during socializing and least likely to occur during travelling. There were no significant interactions between group size and activity type. Signature and probable signature whistles made up *ca.* 52% of all whistles produced by these free-ranging bottlenose dolphins.

Keywords: bottlenose dolphin; *Tursiops truncatus*; signature whistle; vocalizations

1. INTRODUCTION

Bottlenose dolphins (*Tursiops truncatus*) produce a wide variety of vocal signals to respond to and interact with both their group members and their environment. These vocalizations can be grouped into three different categories: broad-band echolocation clicks; broad-band burst-pulsed sounds; and frequency-modulated narrow-band whistles (Caldwell *et al.* 1990). Caldwell & Caldwell (1965) were among the first researchers to investigate the production of whistles in captive bottlenose dolphins scientifically. Their recordings showed that each animal tended to produce a unique whistle when in isolation. Although the whistles were shown to vary in intensity, duration and rate of production, the basic contour (or pattern of frequency changes over time) of each individual's whistles remained the same overall (Caldwell & Caldwell 1965; Caldwell *et al.* 1990).

Because these whistles contained distinctively individual characteristics, they were termed 'signature whistles' (Caldwell *et al.* 1990). These unique features allow spectrograms of the signature whistle of one individual to be visually separated from spectrograms of signature whistles of other individuals and from spectrograms of non-signature whistles (Janik & Slater 1998). Spectrograms of

signature whistles are more accurately classified visually by human observers than by computer methods because humans are more capable of recognizing the general form of the whistle: naturally occurring variations are minimized instead of being the impetus for separate whistle classifications (Janik 1999). Variations that may occur include repetitions and/or deletions of certain whistle parts and changes in whistle duration or the frequency band in which the whistle is produced.

Signature whistles appear to function in the recognition of individuals by others (Caldwell & Caldwell 1965; Caldwell *et al.* 1990; Sayigh *et al.* 1999); playback experiments demonstrated that temporarily captured free-ranging dolphins are capable of discriminating between the signature whistles of different familiar individuals (Sayigh *et al.* 1999). Signature whistles also appear to function in maintaining group cohesion. Janik & Slater (1998) found that captive bottlenose dolphins primarily produced stereotyped signature whistles when one individual was separated from the rest of the group and that the separated individual primarily produced one stereotyped signature whistle. However, when all of the animals were together, they primarily produced non-signature whistles. These data suggest that signature whistles of bottlenose dolphins provide a means of locating and maintaining contact with other dolphins. Similarly, Smolker *et al.* (1993) showed that wild bottlenose dolphin mother–calf pairs whistled commonly while separated, but not as frequently while together.

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McCowan & Reiss (1995, 2001), however, found that 12 captive dolphins shared a variety of whistle types within and among socially interactive groups. Based on these data, McCowan & Reiss (1995) suggested that signature whistles occur only during times of stress, as they had been documented only in small captive groups or in restrained captive or free-ranging animals. In their later study, McCowan & Reiss (2001) suggested that signature whistles do not exist at all.

The goal of this study was to determine whether unrestrained free-ranging dolphins do produce signature whistles, and if they do, to relate this production to factors such as activity and group size. To date, very little research has been done in this area, primarily because of the difficulties in identifying which dolphin is vocalizing. A resident community of bottlenose dolphins near Sarasota, Florida provides a unique opportunity to study signature-whistle production because most of the animals have been recorded during brief capture–release events since 1975 (Wells & Scott 1990). Dolphins tend to produce large numbers of stereotyped signature whistles during capture–release events; thus, these whistles can be compared with those recorded from the same animals under undisturbed conditions. These data provide insights into whether signature whistles occur naturally in free-ranging dolphins.

2. MATERIAL AND METHODS

(a) *Sarasota dolphin community*

The data analysed for this study were collected from a resident community of free-ranging bottlenose dolphins in the waters near Sarasota, Florida (Scott *et al.* 1990; Wells 1991, 2003) during May–August 1994 and May–July 1995. Data were collected as part of a study of vocal development, in which acoustic recordings and focal behavioural observations (Altmann 1974) were made of mother–calf pairs. During focal observation sessions, or follows, selected mother–calf pairs were followed for extended periods, often over the course of several hours. The dataset consisted of 141.25 h of observations and recordings.

Dolphins were recorded as described by Sayigh *et al.* (1993). Briefly, to enable continuous recording two hydrophones with weighted cables were towed, while underway, by a small boat. One hydrophone was connected to a high-pass filter to remove noise from the boat engine. Recordings were made with a Panasonic AG-6400 hi-fi VCR that was capable of recording frequencies up to at least 32 kHz (frequency response of 20 Hz to *ca.* 20 kHz; dynamic range of 80 dB at 3% distortion). Verbal comments describing group composition, mother–calf distance, calf's nearest neighbour, activity, location and group size were recorded onto a third channel at 5 min intervals. Activities included milling, travelling, milling/travelling, feeding or probable feeding, resting and socializing (see Appendix A for definitions). Also noted was the presence of other animals in the area, but not within the group (a group was defined as animals within a 50 m radius of the focal animals). Acoustic localization of individual animals was not used in this study. Photographs were taken to ensure proper identification of the animals being studied (Würsig & Jefferson 1990).

(b) *Whistle classification*

The videotapes containing the data were analysed using Signal/RTSD (version 3.0, Engineering Design, Belmont, MA, USA), a sound-analysis computer program capable of displaying spectrograms in real time. First, we familiarized ourselves with the signature whistles of known group members by examining them in the existing Sarasota Dolphin Community signature-whistle catalogue, which contains the predominant whistle produced by each dolphin during capture–release events. This catalogue currently contains whistles from 134 animals, many of which have been recorded on multiple occasions over periods of up to 27 years.

To determine whether signature whistles are produced by free-ranging bottlenose dolphins, a conservative tally of signature-whistle occurrences was kept as their spectrograms were seen on the computer screen. A signature whistle was defined as a whistle that visually matched the known signature whistle (recorded during brief capture–release events) of an animal identified in the group (figure 1). The remaining whistles were categorized as probable signature whistles, upsweeps or others. A probable signature whistle was classified in either of two ways. First, it could be a repeated (twice or more), stereotyped, whistle that visually matched the known signature whistle of a catalogue animal not positively identified in the group (since the focus of the observations was on the behaviour of the focal mother–calf pair, it was often not possible to identify all group members). Second, a probable signature whistle could be a repeated (twice or more), stereotyped, contour that could be attributed to a group member not in the catalogue. For example, if one member of a group had never been recorded during a capture–release event but a repeated stereotyped whistle that was not in the catalogue was consistently heard when this animal was present, that whistle would be classified as a probable signature whistle. An upsweep was classified as a whistle consisting solely of an increase in frequency over time (figure 2). Many signature whistles consist of repeated upsweeps, as seen in figure 1a–d. However, we were extremely conservative when classifying upsweeps as signature whistles or probable signature whistles, by matching subtle contour variations (e.g. compare the upper portions of the upsweeps in figure 1a,b, and the middle portions of the upsweeps in figure 1c,d, see arrows). Thus, the upsweep category probably includes many signature whistles for which the recording clarity was not sufficient to identify the contour positively. Finally, other whistles were defined as those that could not be characterized, often owing to poor recording clarity.

This methodology was not able to account for any possible instances of non-overlapping whistle imitations that may have occurred. In the case of imitations in which two whistles with the same contour overlapped, the first was classified as a signature, probable signature, upsweep or other whistle (as appropriate), and the second was put in the 'other' category.

Overall percentages for each of the four whistle categories were calculated. For statistical analyses, signature and probable signature whistles were combined into a 'signature' whistle category, and upsweep and other whistles were combined into a 'non-signature' whistle category. To determine how group size and activity type relate to whistle frequency, a log-linear model was constructed with the number of whistles per 5 min interval taken as a Poisson-distributed response (log-linear models of various types are discussed in Agresti (2002)). Group size was taken as a quantitative predictor and modelled in a linear fashion, with the model also including effects for activity type and the interaction between group size and activity type. Additionally, since the data consist of sets of observations (follows) on groups of animals, the set of observations for each distinct group of animals was taken as a collection of repeated
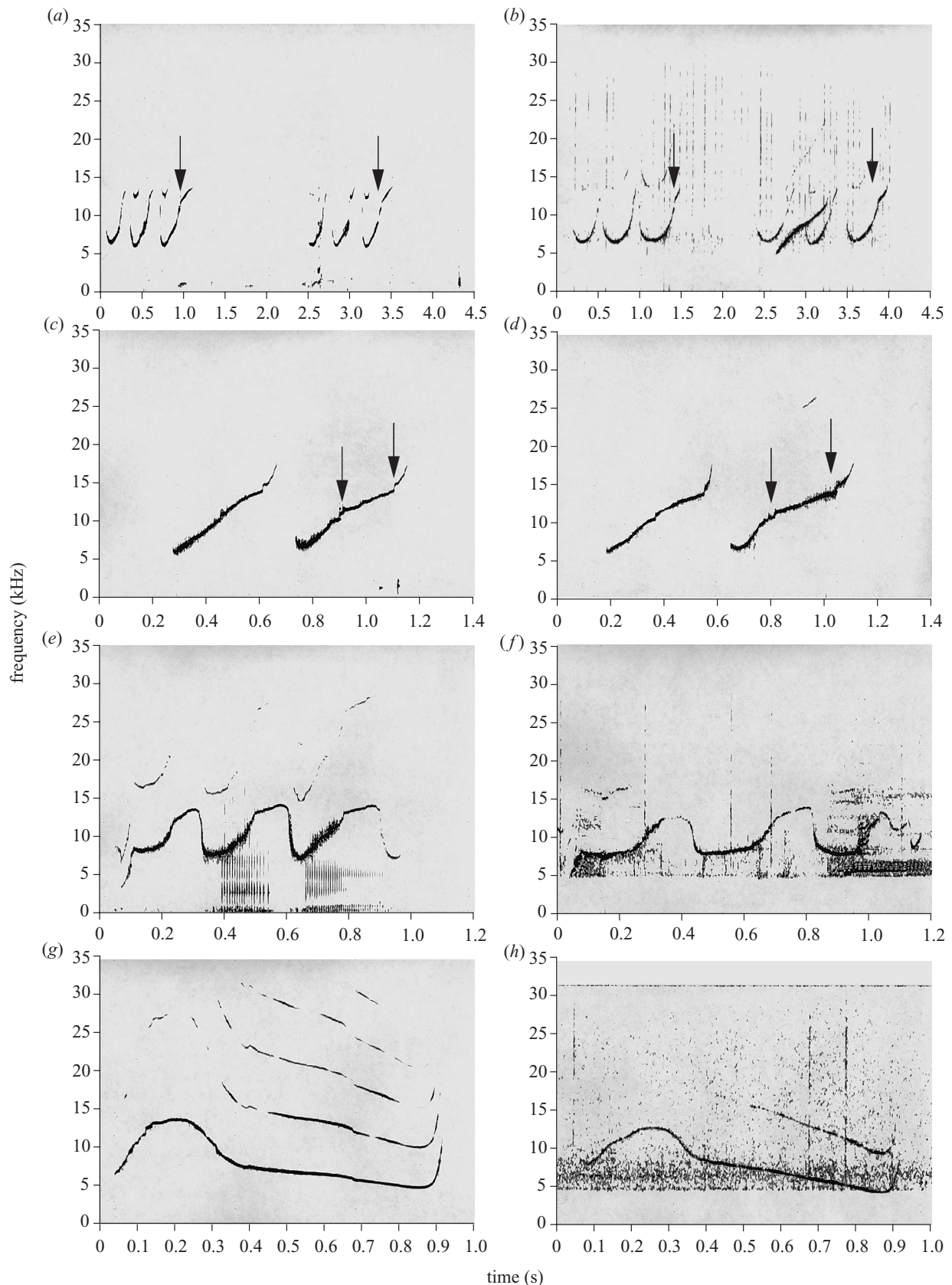
Figure 1. Signature whistles produced by dolphin CLLA during (*a*) a capture–release event and (*b*) a focal follow (this spectrogram also contains a whistle produced by another dolphin); by dolphin FB54 during (*c*) a capture–release event and (*d*) a focal follow; by dolphin F122 during (*e*) a capture–release event and (*f*) a focal follow; and by dolphin FB65 during (*g*) a capture–release event and (*h*) a focal follow. Arrows point to examples of subtle contour variations used when classifying upsweeps as signature (or probable signature) whistles. Spectrograms were made using Signal/RTSD v. 3.0, with a sample rate of 80 kHz, a 512-point fast Fourier transform and a Hanning window.
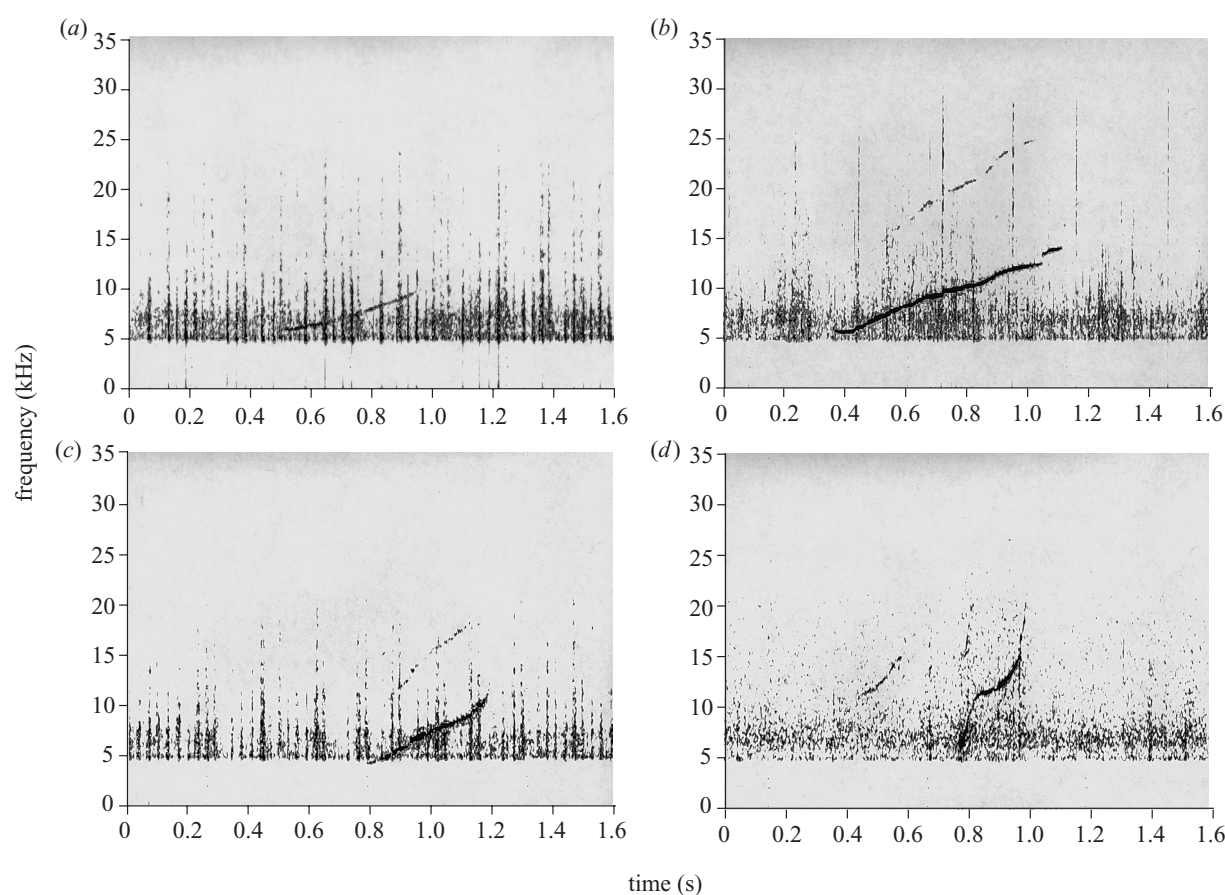
Figure 2. Various whistles classified as upsweeps. Spectrograms were made using Signal/RTSD v. 3.0, with a sample rate of 80 kHz, a 512-point fast Fourier transform and a Hanning window.

Table 1. Test result for the linear relation between signature-whistle rate and estimated group size.

	Z-score	p-value
linear effect of group size	5.46	< 0.0001

Table 2. Test result for the linear relation between non-signature-whistle rate and estimated group size.

	Z-score	p-value
linear effect of group size	5.36	< 0.0001

measures. The p-values for model parameters and multiple comparisons were adjusted for multiplicity of testing using the stepwise Bonferroni–Holm method (Holm 1979). Model fitting and p-value correction were done using the GENMOD and MULTTEST procedures, respectively, from the SAS/STAT software v. 8.2 for Windows (SAS Institute, Cary, NC, USA).

3. RESULTS

Out of the 3208 whistles analysed, 664 (20.7%) were visually classified as signature whistles. Probable signature whistles accounted for 31.5% (1011), upsweep whistles 19.0% (609) and other whistles 28.8% (924). The average number of whistles per 5 min interval was found to be 1.89 ± 0.10 s.e., $n = 3208$.

The results of the log-linear model fits show a significant linear effect of group size, for both 'signature' (signatures plus probable signatures) whistle frequency and 'non-signature' (upsweeps plus others) whistle frequency (tables 1 and 2). There are also significant differences in whistle frequencies across activity types; pairwise comparisons of activity types are contained in tables 3 and 4. The average number of 'signature' whistles per 5 min interval was significantly higher during socializing than during feeding ($p < 0.05$) and significantly lower during travelling than during milling or socializing ($p < 0.05$ for both; table 3). The average number of 'non-signature' whistles per 5 min interval was significantly higher during socializing than during feeding, milling, milling and travelling or resting ($p < 0.05$ for all), and significantly lower during travelling than during feeding, milling, milling and travelling or socializing ($p < 0.05$ for all; table 4). No significant interactions between group size and activity type were detected by the model ($p > 0.11$ for all interaction terms). Additionally, for the purpose of illustration, model-based estimates of whistle frequencies are given for several combinations of group size and activity type (tables 5 and 6).

4. DISCUSSION

Approximately 52% of all whistles produced by free-ranging bottlenose dolphin groups containing mother–calf pairs in Sarasota, Florida are signature or probable signature whistles. Thus, signature whistles clearly are not

Table 3. The χ^2 test statistics and adjusted *p*-values for comparisons of the average number of signature whistles per 5 min interval for each activity type. For each pair of numbers, the χ^2 value is given on top and the *p*-value is given underneath.

	milling	milling and travelling	resting	socializing	travelling
feeding	1.23	0.49	1.18	7.03	2.85
	1.0000	1.0000	1.0000	0.0402	0.1955
milling		0.01	0.19	4.16	9.41
		1.0000	1.0000	0.1241	0.0162
milling and travelling			0.15	2.45	3.01
			1.0000	0.2207	0.1955
resting				1.27	4.93
				1.0000	0.0987
socializing					16.36
					0.0008

Table 4. The χ^2 test statistics and adjusted *p*-values for comparisons of the average number of non-signature whistles per 5 min interval for each activity type. For each pair of numbers, the χ^2 value is given on top and the *p*-value is given underneath.

	milling	milling and travelling	resting	socializing	travelling
feeding	2.25	0.41	3.76	12.49	13.09
	0.7070	1.0000	0.3664	0.0037	0.0030
milling		0.80	1.28	28.07	13.45
		1.0000	1.0000	< 0.0001	0.0027
milling and travelling			2.45	16.61	11.90
			0.7070	0.0006	0.0045
resting				20.89	0.67
				< 0.0001	1.0000
socializing					47.03
					< 0.0001

Table 5. Model estimates of signature-whistle frequencies per 5 min interval. 'Pair', '3–5' and 'more than 5' refer to group sizes.

activity	pair	3–5	more than 5
feeding	0.6557	0.8005	1.1932
milling	0.9420	1.1289	1.6211
milling and travelling	0.5599	1.0686	3.8918
resting	1.0379	1.3717	2.3956
socializing	2.5273	2.8374	3.5766
travelling	0.3376	0.4840	0.9949

Table 6. Model estimates of non-signature-whistle frequencies per 5 min interval. 'Pair', '3–5' and 'more than 5' refer to group sizes.

activity	pair	3–5	more than 5
feeding	0.9518	1.1648	1.7446
milling	0.5318	0.7283	1.3658
milling and travelling	0.5980	0.9040	2.0661
resting	0.3553	0.4684	0.8139
socializing	3.8251	4.4559	6.0468
travelling	0.2314	0.3384	0.7237

merely artefacts of stressful circumstances. The results of our model fits show a significant linear effect of group size for both 'signature' whistle frequency and 'non-signature' whistle frequency; therefore, the whistling frequency of bottlenose dolphins grows at a steady rate as group size increases.

The frequency of 'signature' whistles was higher during socializing than during feeding. While socializing, active interactions among dolphins can occur in one part of the group, while the entire group is often spread out over a wide area. It is possible that as group spread increases vocal contact to maintain group cohesion is more common. Water clarity is poor in this productive estuarine environment, and thus visual contact is generally not feasible over distances of more than a few metres. The frequency of 'non-signature' whistles was also higher during socializing than during several other activities. 'Non-signature' whistles are a promising area for future research, as these results suggest that they may serve a social function.

The frequency of 'signature' whistles was lower during travelling than during milling or socializing. During travelling, animals tend to stay closer together and surface in consistent directions; therefore, physical and/or visual contact may help animals keep track of one another. Thus, the theory that signature whistles are used as cohesion calls (Janik & Slater 1998) is supported by these data. The frequency of 'non-signature' whistles was also lower during travelling than during feeding, milling, milling and

travelling or socializing. This supports the idea that dolphins typically do not use acoustic communication while travelling.

The high whistle rates during socializing (averaging 12 whistles per 5 min interval) were not simply caused by the presence of more dolphins. No significant interactions between group size and activity type were detected by the log-linear model ($p > 0.11$ for all interaction terms). Thus, although socializing often occurs in groups of more than five animals, these findings show that each individual animal in the group is, on average, producing more whistles. Jones & Sayigh (2002) also reported that the average number of whistles per dolphin in Sarasota, Florida was significantly higher while dolphins were socializing than while they were travelling or milling and travelling.

McCowan & Reiss (1995, 2001) concluded that bottlenose dolphins shared certain whistle types, and that the predominant shared whistle type, an upsweep, functioned as a contact call with individually distinct features (McCowan & Reiss 2001). McCowan & Reiss (1995, 2001) also concluded that the use of signature whistles by bottlenose dolphins was rare or even non-existent. However, their studies were conducted with dolphins that were housed in the same tank; if signature whistles function as a means of cohesion, they would not be expected to occur in these circumstances because the animals were never separated from each other by large distances (Janik & Slater 1998; Janik 2000). In addition, good water clarity may enable most captive dolphins to maintain visual contact with one another, thus obviating the need for signature-whistle production.

The present study supports the idea that upsweeps play an important role in the bottlenose dolphin whistle repertoire (Tyack 1986; Janik *et al.* 1994), as 19% of all whistles were classified as upsweeps. However, it appears that the recording conditions of the captive dolphins in the McCowan & Reiss (1995, 2001) studies stimulated upsweep, rather than signature-whistle, production; Tyack (1986) reported that upsweeps comprised only 6% of the whistle repertoires of two captive dolphins. We demonstrated that free-ranging undisturbed dolphins produce a combination of signature whistles and upsweeps in their natural repertoire. The present study clearly demonstrates that signature whistles play an important role in the natural communication system of bottlenose dolphins.

APPENDIX A:

Activities assigned to focal mother–calf pairs and their groups are as follows (Urian & Wells 1996).

(i) Milling—non-directional movement; frequent changes in direction.
(ii) Travelling—directed movement in one direction; not necessarily in a straight line.
(iii) Milling and travelling—combined milling and travelling.
(iv) Feeding—obvious evidence of feeding, for example fish in mouth, diving birds, etc.; this study also included probable feeding, for example lunging.
(v) Resting—quiescent slow movements with no indication of other activities.
(vi) Socializing—active interactions with one or more other dolphins.

REFERENCES

Agresti, A. 2002 *Categorical data analysis*. New York: Wiley-Interscience.

Altmann, J. 1974 Observational study of behavior: sampling methods. *Behaviour* **49**, 227–265.

Caldwell, M. C. & Caldwell, D. K. 1965 Individualized whistle contours in bottlenosed dolphins (*Tursiops truncatus*). *Nature* **207**, 434–435.

Caldwell, M. C., Caldwell, D. K. & Tyack, P. L. 1990 Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. In *The bottlenose dolphin* (ed. S. Leatherwood & R. R. Reeves), pp. 199–234. New York: Academic Press.

Holm, S. 1979 A simple sequentially rejective multiple test procedure. *Scand. J. Statistics* **6**, 65–70.

Janik, V. M. 1999 Pitfalls in the categorization of behaviour: a comparison of dolphin whistle classification methods. *Anim. Behav.* **57**, 133–143.

Janik, V. M. 2000 Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). *Science* **289**, 1355–1357.

Janik, V. M. & Slater, P. J. B. 1998 Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. *Anim. Behav.* **56**, 829–838.

Janik, V. M., Dehnhardt, G. & Todt, D. 1994 Signature whistle variations in a bottlenosed dolphin, *Tursiops truncatus*. *Behav. Ecol. Sociobiol.* **35**, 243–248.

Jones, G. J. & Sayigh, L. S. 2002 Geographic variation in rates of vocal production of free-ranging bottlenose dolphins. *Mar. Mammal Sci.* **18**, 374–393.

McCowan, B. & Reiss, D. 1995 Quantitative comparison of whistle repertoires from captive adult bottlenose dolphins (Delphinidae, *Tursiops truncatus*): a re-evaluation of the signature whistle hypothesis. *Ethology* **100**, 194–209.

McCowan, B. & Reiss, D. 2001 The fallacy of 'signature whistles' in bottlenose dolphins: a comparative perspective of 'signature information' in animal vocalizations. *Anim. Behav.* **62**, 1151–1162.

Sayigh, L. S., Tyack, P. L. & Wells, R. S. 1993 Recording underwater sounds of free-ranging dolphins while underway in a small boat. *Mar. Mammal Sci.* **9**, 209–213.

Sayigh, L. S., Tyack, P. L., Wells, R. S., Solow, A. R., Scott, M. D. & Irvine, A. B. 1999 Individual recognition in wild bottlenose dolphins: a field test using playback experiments. *Anim. Behav.* **57**, 41–50.

Scott, M. D., Wells, R. S. & Irvine, A. B. 1990 A long-term study of bottlenose dolphins on the west coast of Florida. In *The bottlenose dolphin* (ed. S. Leatherwood & R. R. Reeves), pp. 235–244. New York: Academic Press.

Smolker, R. A., Mann, J. & Smuts, B. B. 1993 Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. *Behav. Ecol. Sociobiol.* **33**, 393–402.

Tyack, P. 1986 Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles? *Behav. Ecol. Sociobiol.* **18**, 251–257.

Urian, K. W. & Wells, R. S. 1996 Bottlenose dolphin photo-identification workshop: 21–22 March 1996, Charleston, South Carolina; Final report to the National Marine Fisheries Service, Charleston Laboratory, contract no. 40EUNF500587, National Marine Fisheries Service, Charleston, SC. NOAA tech. mem. NMFS-SEFSC-393.

Wells, R. S. 1991 The role of long-term study in understanding the social structure of a bottlenose dolphin community. In *Dolphin societies: discoveries and puzzles* (ed. K. Pryor & K. S. Norris), pp. 199–225. Berkeley, CA: University of California Press.

Wells, R. S. 2003 Dolphin social complexity: lessons from long-term study and life history. In *Animal social complexity: intelligence, culture, and individualized societies* (ed. F. B. M. de Waal & P. L. Tyack), pp. 32–56. Cambridge, MA: Harvard University Press.

Wells, R. S. & Scott, M. D. 1990 Estimating bottlenose dolphin population parameters from individual identification and capture–release techniques. *Rep. Int. Whaling Commission* **12**, 407–415.

Würsig, B. & Jefferson, T. A. 1990 Methods of photo-identification for small cetaceans. *Rep. Int. Whaling Commission* **12**, 43–52.